THE LYCOTEUTHID GENUS *OREGONIATEUTHIS* VOSS, 1956, A SYNONYM OF *LYCOTEUTHIS* PFEFFER, 1900 (CEPHALOPODA: TEUTHOIDEA)

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Abstract.—Oregoniateuthis Voss, 1956 is placed in the synonymy of Lycoteuthis Pfeffer, 1900. Based on new records, Oregoniateuthis springeri Voss, 1956 is shown to be conspecific with Lycoteuthis diadema (Chun, 1900) and is placed in synonymy. The type of Lycoteuthis lorigera (Steenstrup, 1875) is shown to be a male. Sexual dimorphism in the family Lycoteuthidae is discussed.

Voss (1962) erected a new genus and species, *Oregoniateuthis springeri*, for a single male specimen of a small lycoteuthid squid taken from the stomach of a shark from the Gulf of Mexico. Voss (1962) expanded the description of *O. springeri* based on the holotype (USNM 575090) and a second trawl-collected male (UMML 31.376) from near the type-locality. He also redescribed *Onychoteuthis* (??) *lorigera* Steenstrup, 1875, known only from the type taken from the stomach of a sperm whale from the South Pacific, and placed this species into *Oregoniateuthis*. Voss (1962) considered the possibility that *O. springeri* might be the male of some previously described species; however, the type of *O. lorigera*, reported to be a female, served to validate the genus by sharing with *O. springeri* elongate dorsolateral arms.

Present findings based on new records include an undescribed photophore in female *Lycoteuthis diadema* and show that *O. springeri*, known previously only from males, is conspecific with *L. diadema*, known previously only from females.

A reexamination of the type of O. lorigera shows it to be a male and further demonstrates that Oregoniateuthis can no longer be retained as a separate genus.

The following abbreviations are used: USNM—National Museum of Natural History, formerly United States National Museum, Smithsonian Institution; UMML—Invertebrate Museum, Rosenstiel School of Marine and Atmospheric Sciences, University of Miami; SAM—South African Museum; ORE—M/V Oregon; ORE II—M/V Oregon II; CI—R/V Columbus Iselin; SIL BAY—M/V Silver Bay; IKMT—Issacs-Kidd midwater trawl; FT—flat trawl; ST—shrimp trawl; PT—pelagic trawl; ML—mantle length; GL—gladius length; F(F)—female(s); M(M)—male(s).

Lycoteuthis Pfeffer, 1900

Lycoteuthis Pfeffer, 1900:156. Thamatolampus Chun, 1903:67. Asthenoteuthion Pfeffer, 1912:172. Leptodontoteuthis Robson, 1926:2. Oregoniateuthis Voss, 1956:120.

Diagnosis.—Lycoteuthids with single large photophore embedded in musculature of fin/mantle complex near apex of fins, with 7 additional serially arranged,

rod-like photophores in elongate posterior projection of mantle of males (unknown in *L. lorigera*); dorsolateral arms elongate in males.

Lycoteuthis diadema (Chun, 1900)

Enoplotenthis diadema Chun, 1900:532. Lycotenthis diadema Chun, 1903:569. Oregoniatenthis springeri Voss, 1956:120; 1962:283. (for a more detailed synonymy consult Voss 1962:275).

Material examined.—Holotype of Oregoniateuthis springeri Voss, M, ML = 80 mm, ORE 382, 29°11.30′N, 88°07.30′W, 200 fms, 21 June 1951, 100′ FT, USNM 575090. Other material:—1F, ML = 125 mm (approx.) (GL = 132 mm), CI-256, 23°37′N, 77°06′W to 23°39′N, 77°07′W, 1360 m, in stomach of Synaphobranchus brevidorsalis, 1 Nov 1974, UMML 31.1735.—6FF, ML = 91-88 mm (GL = 96.2-93.5 mm), 35 miles from Port Elizabeth, South Africa, over 100 fms, in stomach of yellowfin tuna, 23 April 1974, S 38, SAM.—13FF, ML = 89-73 mm (GL = 88.0-69.2 mm), ORE II 10906, 29°17′N, 86°36′W, 0-200 fms, 70′ ST, 8 Feb 1970, USNM 730614.—1F, ML = 79 mm (GL = 85.3 mm), between Lamberts Bay and Vandeling Island, in stomach of *Merluccius capensis*, ?May 1974, S 599, SAM.— 3FF, ML = 91-73 mm (GL = 85.2-71.3 mm), ORE II 10907, $28^{\circ}36'N$, $86^{\circ}15'W$, 0-200 fms, 191' ST, 9 Feb 1970, USNM 730615.—1F, ML = 82 mm (GL = 82.5mm), 25°09'N, 80°34'W, in stomach of Merluccius albidus, 19 Aug 1931, USNM 576949.—1M, ML = 98 mm (GL = 73.8 mm), ORE II 11150, 24°17′N, 87°41′W, 0-305 fms, 71' ST, 14 Aug 1970, USNM 730611.-1M, ML = 93.7 mm (GL = 70 mm approx.), ORE 3296, 28°36′N, 89°48′W, 244–520 fms, 21 Aug 1961, UMML 31.376.—3MM, ML = 95-91 mm (GL = 69.5-62.9 mm), ORE II 10907 (sta. data above), USNM 730612.—4MM, ML = 88-85 mm (GL = 69.2-62.8 mm), ORE II 10906 (sta. data above), USNM 730613.—2MM, ML = 86-85 mm (GL = 65.8-64.2 mm), ORE II 11186, 27°49'N, 85°12'W, 0-250 fms, 120' PT, 27 Aug 1970, USNM 730610.—2FF, ML = 56-46 mm (GL = 59.6-47.4 mm), SIL BAY 1198, 24°11'N, 83°31'W, 200 fms, 9 June 1959, UMML 31.228.—1F, ML = 53 mm (GL = 54.5 mm), west and north of Cape Point, South Africa, in stomach of Thunnus alalunga?, 16 Mar 1962, A 30612, SAM.—1F, ML = 9 mm (GL = 9 mm), ALBATROSS, 32°18′N, 63°30′W, Ocean Acre 7-13-N, 0-1500 m, 3 m IKMT, 8 Sept 1969, USNM 726955.

Partial redescription.—In females the posterior tip of the mantle is drawn out into a short tail that is longitudinally cleft ventrally. A single large photophore lies in a pocket in the musculature at the apex of the fins. It is located slightly dorsoposteriorly to the convex surface of the conus of the gladius. The photophore is laterally compressed, convex dorsally and flat to slightly concave ventrally. A layer of densely placed, large, dark reddish-brown chromatophores surrounds it. The opening in the musculature dorsal to the photophore is covered by translucent connective tissue that forms a dorsally directed window for the emission of light.

See Voss (1962) for a more complete description of this and the following species.

Lycoteuthis lorigera (Steenstrup, 1875)

Onychoteuthis (??) lorigera Steenstrup, 1875:473. Oregoniateuthis lorigera.—Voss, 1962:288.

Material examined.—Holotype, M, ML = 180 mm, fraen Kaskelotmave, Sydhavet, Mus. Zool. Skibslaege. Moller. Zoologisk Museum, København.

Partial redescription.—The badly damaged male reproductive organs are small. The remains of 1 to 3 ruptured spermatophores were found in Needham's sac. Only a single set of reproductive organs was found, located on the left side of the animal; however, the poor condition of the visceral complex does not preclude the possibility of paired organs.

The posterior part of the gladius (conus) is now missing.

Discussion.—Two fortuitous discoveries by the writer during investigations of gladius morphology, namely the proper determination of the gender of the type of Steenstrup's O. lorigera and the identification of a previously undescribed photophore in females of Lycoteuthis diadema, prompted a review of the generic relationships of Oregoniateuthis.

Knowledge of the correct sex of the type of *Lycoteuthis lorigera* nullified the single substantial factor that previously substantiated *Oregoniateuthis*; a nominal species diagnosed by elongate dorsolateral arms in the female, a character of males attributable to *O. springeri*.

The photophore at the base of the short posterior mantle projection found in females of *L. diadema* appears to be homologous to the most proximal of the 8 serially arranged photophores found within the much longer mantle projection of males attributable to *O. springeri*. No other lycoteuthids, with the possible exception of *L. lorigera*, have internal photophores similarly located.

A review of capture data revealed that each of 2 sequential net hauls (ORE II 10906 and 10907) contained both a large number of reproductively mature (gravid) females attributable to *L. diadema* (USNM 730614, 67FF and 730615, 15FF) and similarly developed (spermatophores present) males attributable to *O. springeri* (USNM 730612, 4MM and 730613, 13 MM). These capture records suggest a large mating aggregation.

In 5 previous reports that indicate the gender of specimens attributed to either *L. diadema* or *O. springeri* (Chun 1910; Voss 1956, 1962, 1962a, 1967) all *L. diadema* are females, all *O. springeri*, males. Examination of the holdings of the USNM and the UMML also revealed only females of *L. diadema* and males of *O. springeri* (total of over 150 animals).

These combined lines of evidence based on anatomical, behavioral, occurrence and distributional data provide ample grounds to place *O. springeri* in the synonymy of *L. diadema*. Retention of these as separate taxa would require that the males of one and the females of the other have yet to be reported. In light of the distribution and ecology of these animals and the extensive collecting that has been conducted, particularly in the Gulf of Mexico and western Atlantic Ocean, this possibility is untenable.

High levels of sexual dimorphism are known to exist in the Lycoteuthidae based on *Selenoteuthis scintillans*, albeit not as great as now recognized in *Lycoteuthis*. Several important parallels in sex-linked character expression exist between *Se*-

lenoteuthis and Lycoteuthis. Only the males of both genera possess brachial photophores. These are located at the arm tips in S. scintillans and along the aboral surface of the arms in L. diadema. The terminal mantle photophore in male S. scintillans is proportionally nearly twice the size of that found in conspecific females (compare Figs. 12b and 13a in Voss 1962). In L. diadema the posterior mantle (tail) photophores are more numerous in males (8) than females (1). Toll (1982) showed that L. diadema and S. scintillans share sex-linked character expression in 3 gladius indices. Females of both species have greater anterior gladius width and anterior vane length indices while males have a greater free rachis length index.

Sexual dimorphism is well known in other teuthoid families. The males of both *Alloteuthis* and *Uroteuthis* (family Loliginidae) have a more elongate posterior projection of the mantle than do conspecific females. This is similar to the condition now recognized in *Lycoteuthis diadema*. Males of *Berryteuthis anonychus* (family Gonatidae) lack hooks on the arms while conspecific females bear hooks on the basal portions of arms I–III (Roper, Young and Voss 1969). In 6 genera of cranchiids only the females possess brachial end organs (N. Voss 1980). Among non-teuthoid cephalopods, only males of *Sepia confusa* possess a tail-like elongation of the fins (Massy and Robson 1923). Males of *S. incerta* and *S. burnupi* possess specially modified arms (Roeleveld 1972). Sexual dimorphism in the class reaches its greatest expression in the pelagic octopods *Argonauta* and *Tremoctopus* in which the females reach a size in excess of 20 times that of the diminutive males.

Imber (1975) suggested that O. springeri (=L. diadema) may be conspecific with L. lorigera and tentatively placed it in synonymy. This is rejected in light of the significant difference in size at maturity. Imber's use of longimanus as the correct senior synonym of lorigera is seen as based on circumstantial evidence and is not followed here.

Unfortunately, over a century after Steenstrup described *L. lorigera* it remains known from only the type. Further evaluation of its taxonomic affinities must await additional material. Some records of females of *L. diadema* from southern latitudes may be pertinent to future consideration of *L. lorigera*.

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Literature Cited

- Chun, C. 1900. Aus den Tiefen des Weltmeeres.—Gustav Fischer, Jena, viii + 549 pp., 390 figs., 46 pls.
- ——. 1903. Aus den Tiefen des Weltmeeres. Zweite Auflage.—Gustav Fischer, Jena, x + 592 pp., 482 figs., 46 pls.
- ——. 1910. Die Cephalopoden. 1. Teil: Oegopsida.—Wissenschaftliche Ergebnisse VALDIVIA 18(1): 1–401, atlas of 61 pls.
- Imber, M. J. 1975. Lycoteuthid squids as prey of petrels in New Zealand seas.—New Zealand Journal of Marine and Freshwater Research 9(4):483-492.
- Massy, A. L., and G. C. Robson. 1923. On a remarkable case of sex-dimorphism in the genus *Sepia*.—Annals and Magazine of Natural History (9)12:435–442.
- Pfeffer, G. 1900. Synopsis der oegopsiden Cephalopoden.—Mitteilungen aus dem Naturhistorischen Museum 17 (Beiheft zum Jahrbuch der Hamburgischen Wissenschaftlichen Anstalten 17):145–198.
- . 1912. Die Cephalopoden des Plankton Expedition.—Ergebnisse Plankton Expedition der Humboldt-Stiftung 2: 1–815, atlas of 48 pls.
- Robson, G. C. 1926. The Cephalopoda obtained by the S. S. PICKLE. Supplementary Report.— Report of the Fisheries and Marine Biological Survey, Union of South Africa 4(8):1-6, 1 pl.
- Roeleveld, M. A. 1972. A review of the Sepiidae (Cephalopoda) of southern Africa.—Annals of the South African Museum 59(10):193-313, 11 pls., 20 figs.
- Roper, C. F. E., R. E. Young, and G. L. Voss. 1969. An illustrated key to the families of the order Teuthoidea (Cephalopoda).—Smithsonian Contributions to Zoology 13, 32 pp., 16 pls.
- Steenstrup, J. 1875. *Hemisepius*, en ny slaegt of *Sepia*-blaeksprutternes familie, med bemaerkninger om *Sepia*-formerne i almindelighed.—Kongelige Danske Videnskabernes Selskabs Skrifter 5(10):465-482, 2 pls.
- Toll, R. B. 1982. The comparative morphology of the gladius in the order Teuthoidea (Mollusca: Cephalopoda) in relation to systematics and phylogeny.—Doctoral Dissertation, University of Miami, 390 pp., 41 pls., 12 figs.
- Voss, G. L. 1956. A review of the cephalopods of the Gulf of Mexico.—Bulletin of Marine Science of the Gulf and Caribbean 6(2):85-178.
- ——. 1962. A monograph of the Cephalopoda of the North Atlantic I. The family Lycoteuthidae.—Bulletin of Marine Science of the Gulf and Caribbean 12(2):264–305.
- ——. 1967. Some bathypelagic cephalopods from South African waters.—Annals of the South African Museum 50(5):61–88, 9 pls.
- Voss, N. A. 1980. A generic revision of the Cranchiidae (Cephalopoda; Oegopsida).—Bulletin of Marine Science 30(3):365-412, 13 figs.

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